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ABSTRACT

In three forests that differed in annual rainfall and seasonality, the probability of a liana with a stem ≥2.0 cm stem diameter reaching the canopy was >50 percent. Lianas reached the canopy at significantly smaller size-classes (1.5 cm) in the wet aseasonal forest, suggesting that this estimate changes with forest type. Nevertheless, as a general rule, we suggest that 2.0 cm is the minium stem

diameter to examine the abundance and diversity of canopy lianas or canopy competition between lianas and trees.

Lianas (woody vines) are an abundant and diverse growth form in lowland tropical forests, where they play a key role in many aspects of forest dynamics. Lianas can limit tree growth and fecundity, increase tree mortality, suppress gap-phase regeneration, and alter a number of key ecosystem processes (Putz 1984; Stevens 1987; Putz & Mooney 1991; Schnitzer *et al.* 2000; Schnitzer & Carson 2000, 2001; Laurance *et al.* 2001; Schnitzer & Bongers 2002; Pérez-Salicrup *et al.* 2004). Lianas compete intensely with trees for both belowground (*e.g.*, Dillenburg *et al.* 1993, 1995; Pérez-Salicrup & Barker 2000; Schnitzer *et al.* 2005) and aboveground resources by preempting light (Ogawa *et al.* 1965, Clark & Clark 1990, Schnitzer *et al.* 2000). Lianas have been reported to infest the canopies of 32–86 percent of tropical trees larger than 10 cm in diameter (Putz 1983, Putz & Chai 1987, Campbell & Newbery 1993, Pérez-Salicrup *et al.* 2001). The intensity of aboveground competition between lianas and canopy trees may depend on the number and sizes of lianas in the canopy. If lianas with relatively small diameters (*e.g.*, 1–5 cm), which are the most abundant size-classes in old–growth forests (*e.g.*, DeWalt *et al.* 2000, DeWalt & Chave 2004, Mascaro *et al.* 2004), are also common in the canopy, then studies that omit these relatively small lianas may underestimate the contribution of lianas to forest dynamics.

Currently, little is known about the vertical distribution of lianas in tropical forests and the diameter of lianas that are typically present in the canopy. Lianas reach the forest canopy at smaller diameter size-classes than do trees (Putz 1984); therefore, studies that use relatively large minimum diameter size-class cutoffs likely omit some lianas that are present in the canopy, and thus the potential for competition for light between lianas and trees may be underestimated. To address these issues and to further understand the ecology of lianas and the dynamics of competition between lianas and trees, we surveyed lianas over a gradient of size-classes (0.2 to >5.0 cm diameter) in three forests located across the isthmus of Panama that differed in mean annual rainfall, seasonality, and the percentage of deciduous canopy tree species. We quantified the location of lianas with respect to their vertical distribution (whether the crown of the liana was located in the forest canopy, subcanopy or understory) and determined the probabilities of lianas being in the canopy across different size-classes and among the different forest types.

We conducted this study in three lowland tropical forests located along a rainfall and seasonality gradient across the isthmus of Panama (distance *ca* 55 km). The study sites included a dry forest on the Pacific side of the isthmus (Cocoli), a seasonally deciduous moist forest in the center of the isthmus (Barro Colorado National Monument, BCNM), and a wet forest on the Atlantic side (Ft. Sherman). Cocoli experiences a mean annual rainfall of *ca* 1750 mm and has the longest dry season of the three forests (*ca* 129 d; Condit *et al.* 2000; long-term rainfall data from the Meteorology and Hydrology Branch, Panama Canal Authority, Republic of Panama). BCNM receives an average annual rainfall of *ca* 2600 mm and has a moderately long dry season (*ca* 118 d; Condit *et al.* 2000; see also Leigh 1999). The wet forest at Ft. Sherman receives more than 3000 mm of rainfall annually and has the shortest dry season of the three forests (*ca* 106 d; Condit *et al.* 2000). Estimates of the length of the dry season are based on the number of days where potential evapotranspiration exceeds precipitation (data from Condit *et al.* 2000). The percentage of deciduous canopy tree species in the three forests

corresponded to the annual precipitation and seasonality. Only 14 percent of the canopy tree species at Ft. Sherman were deciduous, whereas 28 and 41 percent were deciduous at BCNM and Cocoli, respectively.

At each site, we established plots in which we measured the diameter of the lianas and recorded the location of their crown foliage (see below). At Cocoli and Ft. Sherman, we established eight and nine, 10 × 10 m randomly located plots, respectively, in which we censused all lianas >0.2 cm (measurements taken at 130 cm along the stem from the roots; see Schnitzer 2006). None of the plots at Cocoli and Ft. Sherman were fenced or manipulated. At BCNM, we used 16 previously established rectangular 24 × 36 m plots, which were divided evenly between island and mainland locations. As part of a different study, eight of these plots were fenced in 1994 to exclude mammals. Because there were no significant differences in the average size of lianas entering the canopy between island vs. mainland plots (ANOVA, $P < 0.36$, $F_{3,12} = 0.89$) and fenced vs. unfenced plots ($P < 0.98$, $F_{3,12} = 0.00$), we included all 16 plots in this study. Due to time and labor constraints, we restricted our survey of the BCNM plots to the ten most common liana species, which included the following species: *Coccoloba parimensis* (Polygonaceae), *Doliocarpus major* (Dilleniaceae), *Doliocarpus olivaceus* (Dilleniaceae), *Hiraea reclinata* (Malpighiaceae), *Maripa panamensis* (Convolvulaceae), *Paullinia bracteosa* (Sapindaceae), *Paullinia turbacensis* (Sapindaceae), *Petrea aspera* (Verbenaceae), *Phryganocydia corymbosa* (Bignoniaceae), *Prionostemma aspera* (Hippocrateaceae). These ten species constituted 61 percent of all liana individuals in our plots. In all three sites combined, we sampled a total of 2710 individuals.

We assigned each liana to one of three categories. A “canopy” classification indicated that an individual's crown foliage was located on or above the top of the forest canopy. A “subcanopy” classification indicated that the foliage of the individual liana was located in the forest stratum below the top of the canopy down to 5 m above the forest floor. An “understory” classification indicated that a liana's crown foliage was located within 5 m of the forest floor. We created these canopy classifications because lianas have unique characteristics (*e.g.*, long, thin, looping stems) that make traditional quantitative measurements (*e.g.*, stem diameter or plant length), unsuitable for estimating the location of their crown (see Parker *et al.* 1989, Kohyama & Hotta 1990). A small percentage of lianas in this study (1.6%) were excluded from analyses either because they were in treefall gaps or they had apparently grown into the canopy but had fallen and were in the understory at the time of the census.

At each of the three sites, we calculated the mean proportion of lianas classified as canopy, subcanopy, and understory for each size-class, using the plot as the unit of replication. We selected the following size-classes: 0.2–0.49 cm, 0.5–0.99 cm, increments of 0.5 cm from 1.0 cm to 5.0 cm, and all lianas >5.0 cm. We used logistic regression to determine, for each forest site, the probability of a liana being in the canopy given its stem diameter (SAS Institute 2000, PROC GENMOD, binomial distribution logit link). Significant differences in the relationships between stem diameter and probability of being in the canopy among the forests were evaluated with likelihood ratio χ^2 tests of independence. We also plotted the mean percentage of lianas in the understory, subcanopy, and canopy for each size-class at each forest, as well as for each of the ten most common species on BCNM.

In all three forests, the probability that a liana reached the canopy was >50 percent for lianas ≥2.0 cm in diameter and >80 percent for lianas ≥2.5 cm in stem diameter (Fig. 1). Lianas had a significantly higher probability of reaching the canopy at a smaller size-class at Ft. Sherman than in the other two forests (Ft. Sherman vs. Cocoli: χ^2= 9.99, df = 1, *P*= 0.002; Ft. Sherman vs. BCNM: χ^2= 9.30, df = 1, *P*= 0.002). Lianas at Cocoli and BCNM had similar probabilities of being in the canopy at all diameters (χ^2= 0.21, df = 1, *P*= 0.65). At Ft. Sherman, lianas ≥1.5 cm stem diameter had >70 percent probability of being in the forest canopy; whereas at BCNM and Cocoli, the probability that lianas were in the canopy exceeded 70 percent only when their diameter was greater than 2.0 cm (Fig. 1). In all three forests, the proportion of subcanopy and understory lianas decreased in a predictable manner with increasing diameter, and relatively few lianas >2.0 cm were classified as understory or subcanopy in any of the forests (Fig. 2). This relationship was consistent among the common species on BCNM that were present in the large size-classes (>2.0 cm; data not shown), suggesting that this pattern may be independent of species identity.

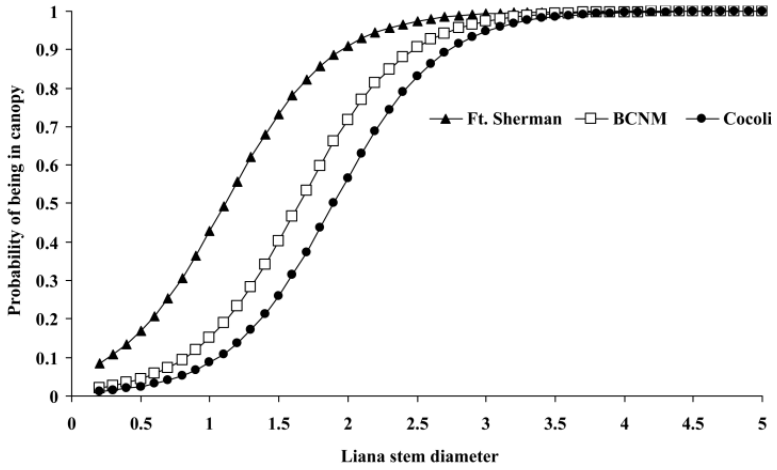

Figure 1 Predicted probability of lianas being in the canopy given their stem diameter for three forests across the isthmus of Panama. Cocoli is a dry forest, Barro Colorado National Monument (BCNM) is a seasonally deciduous moist forest, and Ft. Sherman is a wet forest. Closed triangles represent Ft. Sherman, open squares represent BCNM, and closed circles represent Cocoli. Lianas were significantly more likely to be in the canopy at a smaller size-class at Ft. Sherman than in the other two forests (logistic regression: χ^2= 10.64, df = 2, *P*= 0.005); however, the slopes of the logistic regression did not differ among the forests (stem diameter by forest interaction: χ^2= 2.52, df = 2, *P*= 0.28). In each forest, liana stem diameters were measured 130 cm from the roots.

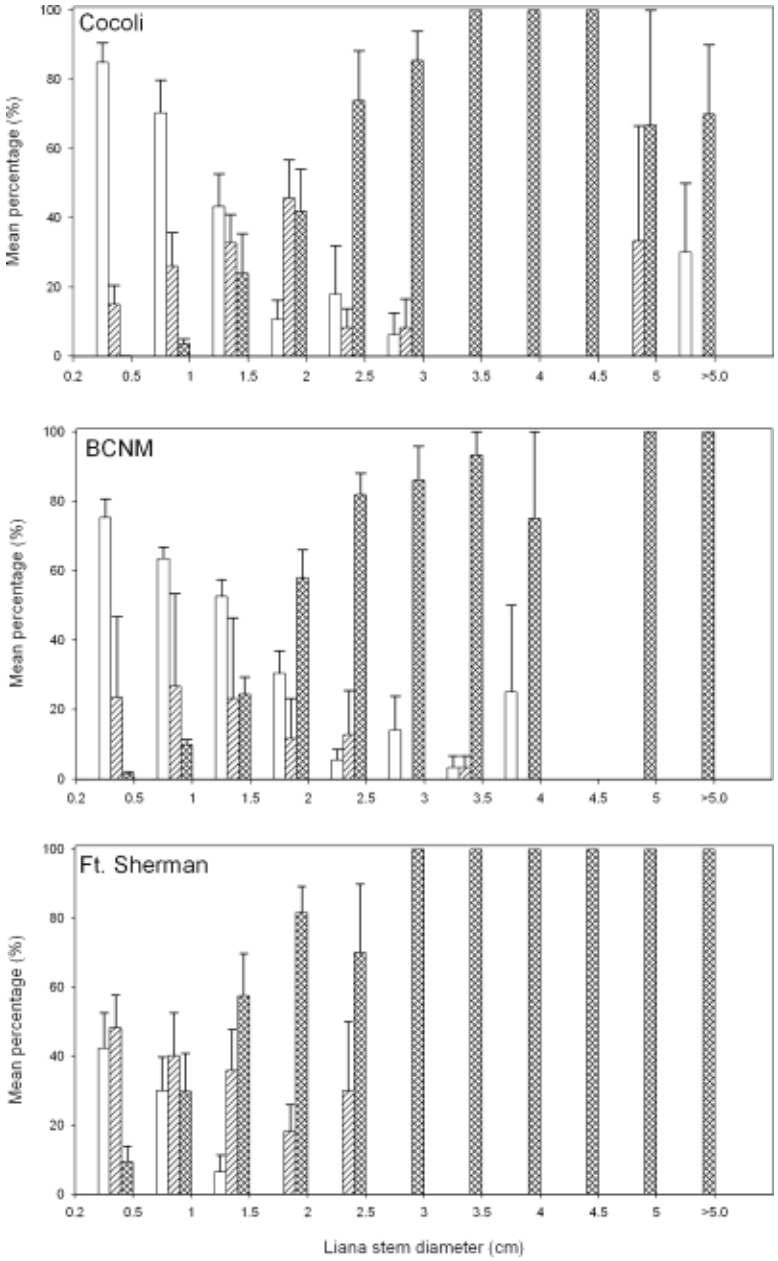

Figure 2 Meanyy proportion of lianas of different stem diameter categories in the canopy, subcanopy, and understory of three forests across the isthmus of Panama. Open bars represent lianas in the understory, single crosshatched bars represent subcanopy lianas, and double crosshatched bars represent canopy lianas. Liana diameters were measured 130 cm from the roots. Replication was at the plot level for all three forests and, for each size-class, the number of replicate plots ≥3, except 4.0–4.49 cm at Cocoli (*N*= 1) and 4.0–4.49 cm (*N*= 0) and 4.5–4.99 cm (*N*= 1) at BCNM. Error bars represent one standard error.

Our findings demonstrate that, in a variety of forests across Panama, a majority of lianas larger than 2.0 cm in stem diameter have their crowns in the canopy. In these same forests, lianas larger than 2.5 cm stem diameter have more than an 80 percent chance of being in the canopy. Correspondingly, relatively few lianas >2.0 cm were in the understory or subcanopy (Fig. 2). These data suggest that 2.0 cm may be used as a general minimum diameter cutoff to include lianas that reach the canopy in lowland tropical forests. This suggestion is consistent with findings of Gerwing and Farias (2000), who reported that lianas 2.0 cm in diameter had, on average, as much leaf mass as small canopy trees (10

cm diameter), and thus lianas 2.0 cm may be comparable to 10 cm diameter canopy trees (see also Gerwing *et al.* 2006). The probabilities that smaller sized lianas (<2.0 cm) were in the canopy, however, differed significantly among the forests. Lianas had a significantly higher probability of reaching the canopy at a smaller size-class in the wet forest of Ft. Sherman than either BCNM or Cocoli. Therefore, the 2.0 cm diameter cutoff could be lowered to 1.5 cm for wet aseasonal forests to include a comparable proportion of canopy individuals (Fig. 1).

The relatively low proportion of small lianas in the understory and subcanopy and the high proportion in the canopy at Ft. Sherman may be due to its darker understory, which results from the relatively thick canopy and few deciduous trees. The change in canopy density between the wet and dry seasons, and the concomitant increase in light that can reach the forest floor during the dry season, is as low as 3 percent at Ft. Sherman, but as high as 20 percent at Cocoli (Condit *et al.* 2000). Because the understory at Ft. Sherman is darker throughout the year, it is possible that fewer liana seeds may germinate and fewer seedlings may survive, thus explaining the relative paucity of lianas in the understory. In direct contrast, the dry forest of Cocoli had the lowest proportion of small lianas (<2.0 cm) in the canopy and the highest proportion in the understory. This pattern may be the result of the relatively high amount of light that reaches the forest floor at Cocoli, especially during the dry season (Condit *et al.* 2000). Higher light levels may enhance liana germination, growth, and survival, which in turn allow more small lianas to persist in the understory (Schnitzer 2005).

An alternative, but not mutually exclusive explanation for the higher proportion of lianas in the canopy of Ft. Sherman is that the height of the canopy of this forest may be lower than that of the other two forests, and thus lianas may be able to reach the canopy at a smaller stem diameter. Ft. Sherman has a mean canopy height of approximately 36 m, whereas BCNM and Cocoli are approximately 42 and 41 m tall, respectively (S. Bohlman, pers. comm.). An additional alternative explanation for the higher proportion of lianas in the canopy of Ft. Sherman may be a greater number of trees in wet forests (Gentry 1991, Schnitzer 2005), many of which are in the understory, serving as trellises that allow lianas to ascend to the canopy at relatively small size-classes.

By quantifying the probability that a liana of a given diameter will be present in the canopy, we provide a reasonable criterion for the minimum size-class for canopy lianas. We recommend ≥2 cm diameter for moist and dry seasonal forests and ≥1.5 cm for wet, relatively aseasonal forests. Studies aimed at understanding the dynamics of forest canopies in a variety of lowland forest types can utilize this minimum size-class for lianas with relative confidence that the majority of those individuals will be found in the canopy. Additionally, our findings may allow researchers to assess better the vertical distribution of lianas in a tropical forest or use only lianas that are likely to be actively climbing to test for liana–host interactions (*e.g.*, DeWalt *et al.* 2000). Because canopy lianas appear to reduce tree growth and fecundity, as well as increase rates of tree mortality (Stevens 1987; Clark & Clark 1990; Schnitzer *et al.* 2000, 2004, 2005; Schnitzer & Bongers 2002), determining the level of liana canopy infestation may result in a clearer picture of the impact of lianas on forest dynamics. Finally, as lianas increase in abundance in tropical forests (Phillips *et al.* 2002, Wright *et al.* 2004), information concerning the vertical distribution of lianas and the extent of competition for light between lianas and trees may become increasingly important.

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References

Campbell , E. J. F. , and D. Newbery . 1993 . Ecological relationships between lianas and trees in lowland rainforest in Sabah. East Malaysia . *J. Trop. Ecol.* **9** : 469 – 490 .

Clark , D. B. , and D. A. Clark . 1990 . Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest . *J. Trop. Ecol.* **6** : 321 – 331 .

Condit , R. , K. Watts , S. A. Bohlman , R. Perez , R. B. Foster , and S. P. Hubbell . 2000 . Quantifying the deciduousness of tropical canopies under varying climates . *J. Veg. Sci.* **11** : 649 – 658 .

DeWalt , S. J. , and J. Chave . 2004 . Structure and biomass of four lowland Neotropical forests . *Biotropica* **36** : 7 – 19 .

DeWalt , S. J. , S. A. Schnitzer , and J. S. Denslow . 2000 . Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest . *J. Trop. Ecol.* **16** : 1 – 9 .

Dillenburg , L. R. , A. H. Teramura , I. N. Forseth , and D. F. Whigham . 1995 . Photosynthetic and biomass allocation responses of *Liquidambar styraciflua* (Hamamelidaceae) to vine competition . *Am. J. Bot.* **82** : 454 – 461 .

Dillenburg , L. R. , D. F. Whigham , A. H. Teramura , and I. N. Forseth . 1993 . Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua* . *Oecologia* **93** : 48 – 54 .

Gentry , A. H. 1991 . The distribution and evolution of climbing plants . *In* F. E. Putz and H. A. Mooney (Eds .). *The Biology of Vines* , pp . 3 – 49 . Cambridge University Press , Cambridge .

Gerwing , J. J. , and D. L. Farias . 2000 . Integrating liana abundance and forest stature into an estimate of aboveground biomass for an eastern Amazonian forest . *J. Trop. Ecol.* **16** : 327 – 336 .

Gerwing , J. J. , S. A. Schnitzer , R. J. Burnham , F. Bongers , J. Chave , S. J. DeWalt , C. E. N. Ewango , R. Foster , D. Kenfack , M. Martínez-Ramos , M. Parren , N. Parthasarathy , D. R. Pérez-Salicrup , F. E. Putz , and D. W. Thomas . 2006 . A Standard Protocol for Liana Censuses . DOI : DOI: 10.1111/j.1744-7429.2006.00134.x .

Kohyama , T. , and M. Hotta . 1990 . Significance of allometry in tropical saplings . *Funct. Ecol.* **4** : 515 – 521 .

Laurance , W. F. , D. Pérez-Salicrup , P. Delamonica , P. M. Fearnside , S. Agra , A. Jerozolinski , L. Pohl , and T. E. Lovejoy . 2001 . Rain forest fragmentation and the structure of Amazonian liana communities . *Ecology* **82** : 105 – 116 .

Leigh , E. G. 1999 . *Tropical forest ecology* , p. 245 . Oxford University Press , New York .

Mascaro , J. , S. A. Schnitzer , and W. P. Carson . 2004 . Liana diversity, abundance and mortality in a tropical wet forest in Costa Rica . *For. Ecol. Manage.* **190** : 3 – 14 .

Ogawa , H. , K. Yoda , K. Ogino , and T. Kira . 1965 . Comparative ecological studies of three main types of forest vegetation in Thailand, 2: Plant biomass . *Nat. Life SE Asia* **4** : 49 – 80 .

Parker , G. G. , O. O'Neill , and D. Higman . 1989 . Vertical profile and canopy organization in a mixed deciduous forest . *Vegetatio* **89** : 1 – 12 .

Pérez-Salicrup , D. R. , and M. G. Barker . 2000 . Effect of liana cutting on water potential and growth of *Senna multijuga* (Caesalpiniodae) trees in a Bolivian tropical forest . *Oecologia* **124** : 369 – 475 .

Pérez-Salicrup , D. R. , S. A. Schnitzer , and F. E. Putz . 2004 . The community ecology and management of lianas . *For. Ecol. Manage. (Special Issue)* **190** : 1 – 118 .

Pérez-Salicrup , D. R. , V. L. Sork , and F. E. Putz . 2001 . Lianas and trees in a liana forest of Amazonian Bolivia . *Biotropica* **33** : 34 – 47 .

Phillips , O. L. , R. V. Martinez , L. Arroyo , T. R. Baker , T. Killeen , S. L. Lewis , Y. Malhi , A. M. Mendoza , D. Neill , P. N. Vargas , M. Alexiades , C. Ceron , A. Di Fiore , T. Erwin , A. Jardim , W. Palacios , M. Saldias , and B. Vinceti . 2002 . Increasing dominance of large lianas in Amazonian forests . *Nature* **418** : 770 – 774 .

Putz , F. E. 1983 . Liana biomass and leaf area of a tierra firme forest in the Rio Negro basin, Venezuela . *Biotropica* **15** : 185 – 189 .

Putz , F. E. . 1984 . The natural history of lianas on Barro Colorado Island, Panama . *Ecology* **65** : 1713 – 1724 .

Putz , F. E. , P. Chai . 1987 . Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia . *J. Ecol.* **75** : 523 – 531 .

Putz , F. E. , and H. A. Mooney . 1991 . *The Biology of Vines* , p. 525 . Cambridge University Press , Cambridge .

SAS Institute . 2000 . JMP statistics and graphics guide, Version 4 . SAS Institute Inc. , Cary , North Carolina .

Schnitzer , S. A. 2005 . A mechanistic explanation for global patterns of liana abundance and distribution . *Am. Nat.* **166** : 262 – 276 .

Schnitzer , S. A. , F. Bongers . 2002 . The ecology of lianas and their role in forests . *Trends Ecol. Evol.* **17** : 223 – 230 .

Schnitzer , S. A. , and W. P. Carson . 2000 . Have we missed the forest because of the trees? *Trends Ecol. Evol.* **15** : 375 – 376 .

Schnitzer , S. A. , and W. P. Carson . 2001 . Treefall gaps and the maintenance of species diversity in a tropical forest . *Ecology* **82** : 913 – 919 .

Schnitzer , S. A. , J. W. Dalling , and W. P. Carson . 2000 . The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration . *J. Ecol.* **88** : 655 – 666 .

Schnitzer , S. A. , S. J. DeWalt , and J. Chave . 2006 . Censusing and measuring lianas: A quantitative comparison of the common methods . *Biotropica* , in press .

Schnitzer , S. A. , M. Kuzee , and F. Bongers . 2005 . Disentangling above- and below-ground competition between lianas and trees in a tropical forest . *J. Ecol.* **93** : 1115 – 1125 .

Schnitzer , S. A. , M. P. E. Parren , and F. Bongers . 2004 . Recruitment of lianas into logging gaps and the effects of pre-harvesting climber cutting . *For. Ecol. Manage.* **190** : 87 – 98 .
Stevens , G. 1987 . Lianas as structural parasites: The *Bursera simaruba* example . *Ecology* **68** : 77 – 81 .
Wright , S. J. , O. Calderon , A. Hernandez , and S. Paton . 2004 . Are lianas increasing in importance in tropical forests? A 17-year record from Barro Colorado Island, Panama . *Ecology* **85** : 484 – 489 .